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DR. WEISMANN ON HEREDITY AND PROGRESS.

I PROPOSE to consider Professor Weismann's views on heredity and progress as set forth in his recently published volume on the "Germ-Plasm" and elsewhere. But I must consider them here rather in their broad and philosophical aspect than in minute biological detail. Those who are endeavoring to frame a monistic interpretation of nature cannot afford to pass by the matured conclusions of a thinker distinguished alike by his mastery of facts and his power of bold, keen, and fearless speculation. But what they want is the net result of his observation and thought, that they may appreciate its bearing on philosophy in general and monism in particular. And if I find cause to criticise some of Dr. Weismann's conclusions I shall here base my criticism not on specifically biological or histological grounds, but on general or *a priori* considerations; for though it is folly to reject a carefully observed fact on *a priori* grounds, it is in accordance with sound method to submit a theory or hypothesis to *a priori* criticism, which is indeed the testing of the congruity of the hypothesis in question to the whole body of philosophical knowledge which constitutes the interpretation of nature which the critic has been led to accept.

Taking the question of heredity first, let us select three well-known facts of organic life and see how Dr. Weismann explains them—always remembering that he puts forward his explanation nowise dogmatically but with due modesty and reserve. The three facts I speak of are, first, the development of the higher animal or plant from a fertilised egg-cell; secondly, the development of certain animals or plants from buds; and thirdly, the regeneration of

lost parts. This regeneration, to take that first, is seen both in the unicellular and in the multicellular organisms. If the oral or mouth-end of one of the infusorians be excised, this portion will be reproduced and the perfect infusorian reconstituted. It would seem to be essential that the part in which the missing parts are thus regenerated should contain a fragment at least of the nucleus of the cell which constitutes the protozoan animalcule. So that we may say that in this case a mutilated fragment of an infusorian cell possesses the potentiality of reconstituting by assimilation and growth the perfect unicellular organism. If a fresh-water hydra be cut in two and the two parts carefully watched, that which contains the base of attachment will be seen to regenerate a new mouth and tentacles, while that which contains the mouth and tentacles acquires a new base of attachment. Or, if the hinder "horn" of a snail—that at the end of which is the eye—be snipped off, a new horn, with a new eye perfect in all its parts, will be regenerated in a few weeks, the exact time varying with the temperature and the age of the snail. And this will occur not once only, but many times in succession. The group of cells which remain to a mutilated hydra or snail possess the potentiality of reproducing by assimilation and growth the perfect multicellular organism.

The same animal, the fresh-water hydra, will afford us a sufficient example of reproduction by budding. Under favorable conditions of temperature, with abundant nutrition, a little protuberance makes its appearance in the tubular body of the polype. This grows rapidly, and gradually assumes the form of a smaller hydra attached to the parental organism. After a while it becomes detached as an independent individual. The body-wall of the hydra consists in the main of two layers, an outer layer composed of large conical cells with small interstitial cells between the points of the cones, and an inner layer of nutritive cells, the two layers being separated by a thin supporting lamella. And it would seem that the bud takes its origin from the interstitial cells of the outer layer. Dr. Weismann indeed assumes that it takes its origin from a single cell of the interstitial series; and it is somewhat characteristic of his method that the assumption once made rapidly takes the form of a statement of

fact. "Each bud," we read, "must originally arise from *one* cell only, although the fact has not yet been actually proved"; and then, half a dozen lines further down, we have: "In the *Hydromedusæ*, then, each bud originates in a single cell." The admittedly unproved assumption already poses as a fact. The assumption itself, however, is not an improbable one; and if we grant its validity we may say that in the hydra a single interstitial cell has the potentiality of producing under appropriate conditions an organism similar to the parent.

Passing to the sexual method of reproduction we find the essence of the process to lie in this, that a single egg-cell produced by an organism unites and coalesces with a single sperm cell produced generally but not invariably by another organism of the same species, and that the fertilised ovum thus produced has the potentiality of producing under appropriate conditions an organism resembling the parents. In certain rare cases, where parthenogenesis obtains, fertilisation does not occur, but the ovum alone possesses the potentiality of reproducing an organism like the parent.

Now the problem is, in all these cases, to give something like a scientific explanation of what I have termed potentiality—the potentiality in the divided protozoan cell of reconstituting the perfect unicellular organism; the potentiality in the mutilated snail of regenerating a lost tentacle; the potentiality in certain interstitial cells of the hydra of giving rise, by cell-multiplication and differentiation, to young hydras; the potentiality in the fertilised egg of reproducing an organism like the parent. What is this potentiality? What is there actually present in the cell or cells concerned which may afford an embryonic basis for the changes which under appropriate conditions, follow in orderly sequence?

In presenting the answer which Professor Weismann gives, let us take first the case of the unicellular organism. This consists of a central nucleus, and of a cell-body. The latter exhibits observable differentiations of structure; but it is by the former, the nucleus, that these differentiations are controlled. The nucleus, therefore, contains, according to Professor Weismann, a store of specialised particles which are the bearers of the peculiar morphological qual-

ities of the cell-body. These particles he terms *biophors*. The biophors are to molecules what molecules are to atoms. Just as the molecule is due to the combination and grouping of atoms to form a higher *physical* unit, so is the biophor due to the combination and grouping of molecules to form a higher *biological* unit. They are the smallest units which exhibit the primary vital forces, assimilation and metabolism, growth, and multiplication by fission. With such biophors, then, the nucleus of the protozoa is stored. "In the unicellular forms heredity will therefore depend, firstly, on the fact that all the different kinds of biophors which are required for the construction of the body are present in the nucleus in a latent condition and in definite proportions—very probably they have also a definite style of architecture; and secondly, on the periodical or occasional migration of these biophors into the cell-body, where they multiply and become arranged in obedience to the forces acting within them. The difficulty of ascertaining the actual mode of arrangement is nowhere greater than in the case of the higher unicellular forms. How it is possible that the nucleus should allow only those kinds of biophors to migrate which are required to replace those structures lost by division? And why do these biophors always move either in the direction of the missing oral region, or towards the posterior end of the body, according to which parts are wanting in the two daughter-animals? For the present these questions are unanswerable; and in the meantime we must be content with having shown how the materials for the construction of the cell-substance are transmitted from mother to daughter, and in what way they are placed at the disposal of the forces acting in the cell-body."

We may say, then, that in the reconstruction of a divided protozoön the potentiality is due to the assumed presence in the nucleus of hypothetical biophors. Of the nature of the forces which act upon the biophors and render reconstruction possible we know little or nothing. It is clear that we have not got much beyond our potentiality. Nevertheless, the conception of biophors is likely to be helpful.

In the multicellular organisms we have an assemblage of independently and hereditarily variable parts; but the number of these

independently variable parts, though great, falls very far short of the vast number of individual cells of which the organism is composed, for, in the first place, there are the multitudes of practically identical cells, such, for example, as the blood-corpuscles, and, in the second place, many of these parts consist of groups of cells, such, for example, as the spots on some butterflies' wings. Dr. Weismann assumes that for each independently variable type of cells, or groups of cells, there exists in the fertilised ovum a *determinant*, that is, a vital unit of a higher order than the biophor, consisting of a group of biophors, and possessed of special qualities. As cell-division proceeds, these determinants are distributed, and when they reach their final destination in the course of development, they break up or disintegrate into their constituent biophors and thus determine the structure of the ultimate cells. These determinants are capable of multiplication by fission; and hence a relatively limited number of these units suffice for the determination of the relatively limitless number of cells in the completed organism.

Here again, without undervaluing the suggestiveness of the hypothesis, we have to notice that what is really the essential problem—the distribution of the determinants during cell-division—remains untouched. In place of the vague potentiality of the fertilised ovum we have certain hypothetical structural units, the determinants. How the potentiality is distributed, and how the determinants are distributed, are alike unknown. It is clear that we have not got much beyond our potentiality. Nevertheless, the conception of determinants, as an attempt to think along physical lines, is to be welcomed.

With regard to the budding of such an organism as the Hydra, Professor Weismann has not much to offer that is helpful towards the solution of the problem. What he does offer practically comes to this: Since an interstitial cell has the potentiality of giving rise to a new Hydra, such cell must have, in an inactive form, all the necessary determinants. *Voilà tout!* So, too, with regard to the regeneration of lost parts. The cells which remain are assumed to possess supplementary determinants for the reconstruction of the

parts which are lost. There is but little advance here on the old-fashioned potentiality.

It must be remembered that we are regarding the matter from a standpoint which only permits a very broad and general view. There is in Dr. Weismann's work a great deal of accurate and suggestive biological detail, which gives to his whole treatment of a difficult subject a value which is well worthy of the generous welcome which it has received. And if in endeavoring to pierce to the hidden cause of hereditary transmission he has failed to do more than suggest that the transmitted potentiality is due to transmitted biophors and determinants, this does but show how far even our leading biologists still are from being able to give a detailed explanation of the mysteries of organic development. As was to be expected from a student of morphology, the suggested explanation is mainly structural, though references to the unknown forces at work are not omitted. And this, no doubt, in the present state of scientific knowledge, is the wiser course. There can be little doubt that structure is merely the visible expression of the subtle play of invisible forces; but we are wise to focus our attention first on the structure and then endeavor to pierce to its hidden cause. Still there is perhaps too great a tendency on Dr. Weismann's part to lay too much stress on the transmission of material particles, too little stress on the transference of subtle modes of energy. He assumes that each vital unit, from the lowest to the highest, can only arise by division from another like itself, and is, therefore, forced to attribute the regeneration of lost parts in the unicellular organism to migration of biophors from the nucleus, saying that such regeneration cannot be the result of the emitted influence of the nuclear substance. This is so, on the assumption adopted; and it may be so in nature. But it is possible that the reconstitution is due to the play of molecular forces and is analogous on the biological plane, to the reconstitution of a chipped crystal on the physical plane.

I must now pass to the second division of my subject, namely, a consideration of Professor Weismann's latest views on progress; and here it will be well to confine our attention to those higher animals which multiply by the sexual process, each individual taking

origin in a fertilised ovum. The ovum and the sperm by which it is fertilised alike contain germ-plasm; and this germ-plasm is stored with determinants of common derivation by multiplication with those, the distribution and disintegration of which gave rise in development to the parental organisms. We may put the matter diagrammatically thus: The compound nucleus of the fertilised ovum is divided into two parts of similar potentiality. Of these, one, through the distribution and disintegration of the contained determinants, gives rise to the developing organism. The other, increased in volume through nutrition and growth and subdivided into ova and sperms, is retained by that organism in the undistributed condition, to subserve the purposes of further reproduction. Now progress depends on variation; and the question here is:—how do effective variations arise? By effective variations I mean those in virtue of which the offspring is raised, in any particular respect, beyond the maximum in either parent or in any ancestor. We may distinguish two kinds or phases of progress. First, progress through the selection of existing maxima; secondly, progress beyond the existing maxima. The latter involves variations of the kind which I have here termed effective. It is obvious that in the evolution of the existing forms of life such variations must again and again have occurred. How do they originate? To what are they due?

Let us first note that no process of selection of maxima or elimination of minima can of itself give rise to effective variation. All it can do is to lead to breeding from maxima only. But, of course, if the maxima are raised through effective variation, *then* selection or elimination may conduce to interbreeding between these new maxima and thus lead to effective progress. Secondly, let us notice that no getting rid of determinants, through differential division, either in the process of the multiplication of the cells which contain the germ-plasm, or in the process known as the “extrusion of the polar cell,” or in any analogous process in the division of sperms, can of itself contribute to effective variation. Such effective variation must depend, according to Professor Weismann’s principles, on the production of new and more highly evolved determinants. Again we must note that no mingling of determinants from

different sources can lead to effective variation, or the genesis of more highly evolved determinants. At one time Dr. Weismann was inclined to attribute effective progress to that mingling of the nuclear matter of ovum and sperm in sexual reproduction to which he has applied the term *amphimixis*. Some three years ago the present writer drew attention to the fact that what he now terms effective progress could not be so accounted for. Other writers have insisted on the same fact. And now Dr. Weismann himself says that "the origin of a variation is equally independent of selection and of *amphimixis*."

To what then does Dr. Weismann attribute effective variation? "It is due," he says, "to the constant recurrence of slight inequalities of nutrition (the term 'nutrition' being used in its widest sense, so as to include differences in temperature, etc.) in the germ-plasm which effect every determinant in one way or another, and differ even in the same germ-plasm,—not only in different individuals but also in different regions." "We cannot possibly attribute," he further says, "the immense number of adaptations to rare, fortuitous variations, occurring only once. The necessary variations from which transformations arise by means of selection, must in all cases be exhibited over and over again by many individuals." They seem to be due to "the permanent action of uniform changes in nutrition." "We are therefore undoubtedly justified in attributing the cause of variation (in varieties of plants which have originated from seeds) to the influence of changed external surroundings."

How changes of nutrition produce particular variations in the determinants of the germ-plasm Dr. Weismann has not pretended to say.

Dr. Weismann remains as firmly convinced as ever that characters acquired by the individual are not, and on his interpretation cannot be, transmitted to that individual's offspring. All variations arise endogenously within the germ-plasm; there is no transference to the germ-plasm of exogenous somatic variations impressed upon or evoked in the muscular, nervous, epithelial, or other tissues of the body. In this he is quite logical and consistent. And he is in my opinion right in maintaining that there is at present no conclu-

sive evidence in favor of such transmission of acquired characters. Facts or groups of facts with a general tendency in that direction there may be ; but definite proof, in my judgment, at present there is not. If such proof should eventually be forthcoming, it will be difficult to resist the conclusion that the determinants of the germ-plasm, if such exist, are subject to the influence of the complex transformations of energy which take place in the somatic tissues. It is more readily conceivable that the determinants are modifiable by the functional activity of parts which originate by the distribution and disintegration of similar determinants, than that they are modifiable by material particles, biophors or other, transmitted to the germ-plasm from the varying somatic parts. All such speculations are, however, at present, premature.

We may now sum up in a few words the salient features of Dr. Weismann's views on development, heredity, and progress, in so far as they apply to the higher animals. (1) The development of the individual from a fertilised ovum is essentially germinal ; that is to say the compound nucleus already contains in the form of determinants the germs of all the varied parts of the complex organism into which it will develop. (2) Heredity is provided for by the constant holding in reserve of some of the germinal matter which increases by growth and cell division, portions thereof being periodically detached in the form of ova and sperms. (3) Effective variation, on which progress through natural selection depends, is provided for by the influence of "nutrition" upon the determinants contained in this reserve germ-plasm.

The first of these propositions is a modern restatement of the old hypothesis of "evolution"—this word being here used in a sense different from that which is to-day in every one's mouth. "Evolution" here means unfolding ; and is applied to the view that the potentiality of development of the fertilised ovum is due to the existence therein of miniature parts exactly resembling those of the adult. It is opposed to "epigenesis" concerning which Professor Weismann says : "I tried in several ways to arrive at a satisfactory epigenetic theory, which, starting from a germ-substance of comparatively simple structure, should exhibit the various differentiations of

the organism as due to regular changes brought about by the division of this primary structure. But the more I considered the problem as time went on, the more I was convinced that such a solution was impossible." This I take it is a distinct and total rejection of epigenesis. And in the light of this complete rejection of epigenesis we may infer what a determinant is. It is, in the first place, a particle of germ-plasm which corresponds to and determines the cells or groups of cells which are independently variable. Let us suppose that my finger-nail is an independently variable part, the product of a single determinant. Then if the nail was formed by "evolution" and nowise epigenetically, its determinant contained in miniature all the minute details of its structure, only *enfolded* and not yet *unfolded*. So that, in the second place, the determinant though it is not a miniature of the fully formed part, contains enfolded miniature germs of all the details of that part. Every detail is already present, but the details are not yet marshalled and ordered. And in general all the details of the adult (with the exception of those which are due to repetition and could thus arise by multiplication) are represented in the nucleus of the fertilised ovum.

It is questionable whether this structural thesis can be maintained either biologically or physically. But it is when we come to consider the energy rather than the matter, that the conception of "evolution" (unfolding) seems to me completely to break down. It is inconceivable that in the compound nucleus of the fertilised ovum there exist in miniature all the varied modes of energy that characterise the life of the adult organism. We are forced to believe that this complex energy arises epigenetically from the simpler energy of the ovum. And if there is this epigenetic development of energy, it is reasonable to infer that there is an epigenetic development of the structure which manifests this energy. I believe therefore that the first of the three propositions is unsound at the core and should be rejected.

The second proposition, if it be held to involve an absolute distinction between germ-plasm and body-plasm, is of doubtful validity. But if it be taken broadly as a statement of the view that cer-

tain cells remain comparatively undifferentiated and retain the potentiality of reproduction, it may be accepted.

The third proposition, that effective variation is due to the influence of nutrition upon the determinants contained in the reserve germ-plasm, seems to throw too much stress on the nutrition and environment, too little on the inherent activities of living matter. But if it be regarded as an expression of the fact that all effective variation is a joint product of the inherent activities of germinal cells and the conditioning effects of their environment, it is a self-evident proposition which may be cheerfully accepted.

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